The Biology of Particles in Aquatic Systems

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Chapter 9

Zooplankton Particle Selection and Feeding Mechanisms

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TABLE OF CONTENTS

I. INTRODUCTION

A. SOME INTERESTING NARRATIVES

Landau[1] has pointed out that scientific theories are essentially narratives and that we have certain basic stories, or deep structures, we tell to organize our experiences. Moreover, she showed how narrative analysis was useful to explain competing theories of the evolution of Man. Feeding, on one hand, and not being killed in predatory encounters, on the other hand, are two important forces in the survival of individuals and evolution of communities. Our subjects of study, the plankton, are heroes in a narrative of life and death, and we scientists are the storytellers.[2] Rather than avoiding narratives, Landau[1] suggests scientists use them, as they are in literature, as a means of discovery and experimentation. Moreover, she notes that recognition of scientific paradigms as narratives or myths is useful because it keeps us from taking them so seriously, thus promoting discovery.

I have begun this chapter on feeding mechanisms of suspension-feeding zooplankton with a reference to narrative because feeding mechanisms have played a central role and will continue to play a central role in the ecological stories we tell about aquatic communities. No study of mechanisms is ever free of an ecological context, and the soundness of our ecological stories can be evaluated only by their consistency with observed mechanisms. Some examples of popular narratives for which understanding of feeding mechanisms is essential for evaluation are:

1. Suspension-feeding zooplankton are optimal foragers who will track peaks in particle-size spectra, i.e., focus their feeding efforts on the most abundant particles.[3,4]

2. The dynamics of pelagic ecosystems can largely be described from knowledge of the size of their components (algae, zooplankton, and fishes) and food-size preferences.[5,6]

3. The microbial food web is a "sink" and not "link" to components of the classic food web (large phytoplankton, large zooplankton, and fishes) because suspension-feeding metazoans cannot efficiently graze picoplankton (<2 μm).[7,8]

Other kinds of narratives about food webs we are likely to tell can be motivated by examination of data from the Laurentian Great Lakes and recent observations and theory connecting micropatchiness and turbulence to the feeding and recruitment success of zooplankton.[9-13] Figure 1 shows that the different Great Lakes exhibit different seasonal patterns of phytoplankton concentration (expressed as chlorophyll a) ranging from ultraoligotrophic Lake Superior, which exhibits a stable and low phytoplankton concentration, to eutrophic lakes Ontario and Erie, which exhibit high and wildly fluctuating phytoplankton concentrations.[14-18] In large part, these concentrations reflect the different nutrient supplies to the lakes. In addition, these lakes — all interconnected — have very different food webs. As we move along the gradient of increasing eutrophy, we see that the crustaceans, first dominated by calanoid copepods, become dominated by cladocerans and cyclopoid copepods (Figure 2).[19-22] As we shall see later, feeding mechanisms probably account for this difference. Note especially the very different food webs in Lake Michigan and Ontario, both of which have the same mean depth (Figure 2) and temperature regimes.

It is probable that zooplankton are adapted to exploit food patches in a temporally and spatially variable environment.[23] There is great interest now in the dual role of wind-generated water turbulence in increasing feeding by increasing encounter rates between zooplankton and particles and decreasing
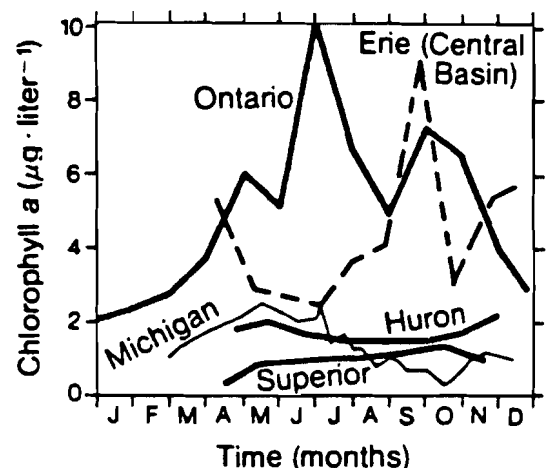
Figure 1. Seasonal chlorophyll a concentrations in the Great Lakes compiled from survey studies of the early 1970's.[14-18] All data are for the epilimnion except the Michigan data, which are integrated over 100 m.
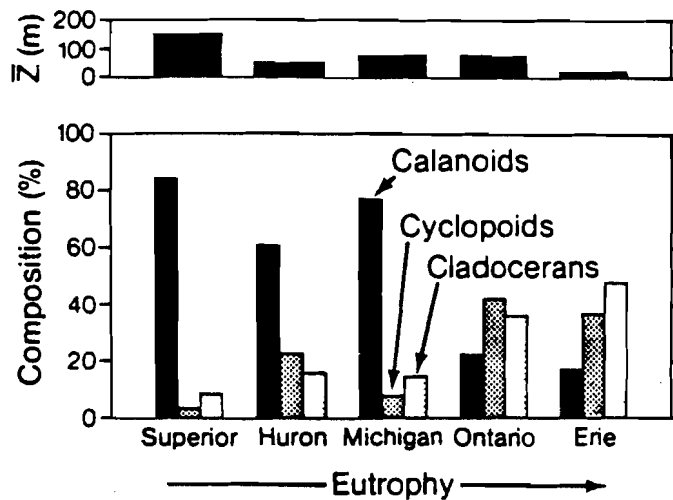
Figure 2. Biomass composition of crustacean zooplankton from early spring through late fall from seasonal survey data.[19-21] Dry weights of Hawkins and Evans[22] were used to convert number concentrations to biomass. Upper panel shows mean depths ($\bar{Z}$) of the lakes.

feeding by destroying patches of particles.[11-13,24] Feeding mechanisms may determine whether turbulence in large water bodies like the Great Lakes is beneficial or detrimental.[25]

B. MATHEMATICAL FRAMEWORKS AND SPECIFIC QUESTIONS
1. Components of Nutrition

All the narratives described above are just submodels of larger food-web models that incorporate zooplankton-particle interaction. It can be argued that the goal of research on feeding mechanisms is the development of mathematical models that predict the feeding rate of zooplankton on all the particles in nature and their subsequent utilization by the zooplankter. These particles would include not only (1) algae of various morphologies, toxicities, and digestabilities, (2) microzooplankton, and (3) detritus, but also (4) inert mineral suspensoids such as clay and autogenically precipitated calcite.[26,27] The presence of large inert particles can lower ingestion rates, and ingested inert particles can lower the assimilation efficiency of carbon in ingested food.[26-28] Resuspended bottom sediments may be a source of toxic chemicals to zooplankton if these sediments are polluted.[26,27]

Recently, Vanderploeg et al.[23] formalized the process of feeding and utilization of ingested food as "components of nutrition" in a fashion analogous to Holling's "components-of-predation" approach (Figure 3).[29] In Figure 3, the components of nutrition can be broken down into two sets, Holling's "components of predation" and "components of utilization", the sequence subsequent to ingestion that leads to growth and reproduction. Some key variables that control each component of nutrition are shown next to the components. Note also connections of certain components with biogeochemical cycling, the loss of C, N, P, and other material to the water. A rather detailed mathematical model could be developed by considering the effects of all controlling variables on each component. My purpose here is, rather, to use it as a framework to organize our thinking about the feeding process. My emphasis is focused on particle choice as it relates to particle quality and important controlling variables, i.e., I am primarily concerned with components of predation.

Holling[29] broke the feeding process into a sequence of chronological steps involving different mechanisms. The probability (P_i) that ingestion of the ith kind of prey ultimately occurs is:

$$P_i = P_{E_i} \cdot P_{A_i} \cdot P_{C_i} \cdot P_{I_i} \tag{1}$$

where P_E, P_A, P_C, and P_I are the conditional probabilities of encounter, attack, capture, and ingestion, respectively. For example, we may think of a pelagic suspension feeder like a copepod that has a volumetric search (foraging) rate, i.e., a searching clearance rate, of ψ. The feeding rate, G_i (units: biomass per time), on the ith prey is

$$G_i = \psi \cdot P_i \cdot X_i \tag{2}$$

where X_i is the concentration of prey (units: biomass per volume). Combining Equations 2 and 1

Figure 3. Components of nutrition and key variables that affect them. The components of nutrition apply to the feeding of a particular life stage of a particular zooplankter. Most zooplankton appear as both predator and prey on this diagram. Control variable abbreviations are: FQ, food quality; M, motivation; WM, water motion (turbulence); NQ, nutritional quality; I, ingestion rate (including history); EC, environmental cues. Shaded boxes refer to "components of predation".[29] The unshaded boxes are "components of utilization". (Redrawn from Vanderploeg, H. A., Checkley, D. M., Jr., Deibel, D., et al., in *Zooplankton Population Biology,* Tessier, A. and Goulden, C. E., Eds., Princeton University Press, Princeton, NJ, in press.)

Controlling variables — Components of nutrition

FQ, M, WM — ENCOUNTER / SEARCH

FQ, M — ATTACK — ESCAPE / REJECTION

FQ, M — CAPTURE — SLOPPY FEEDING

FQ, M — INGESTION — *Biogeochemical Cycling*

NQ, I — ASSIMILATION — EGESTION

NQ, I, WM — METABOLISM

NQ, I, EC — GROWTH, STORAGE, REPRODUCTION
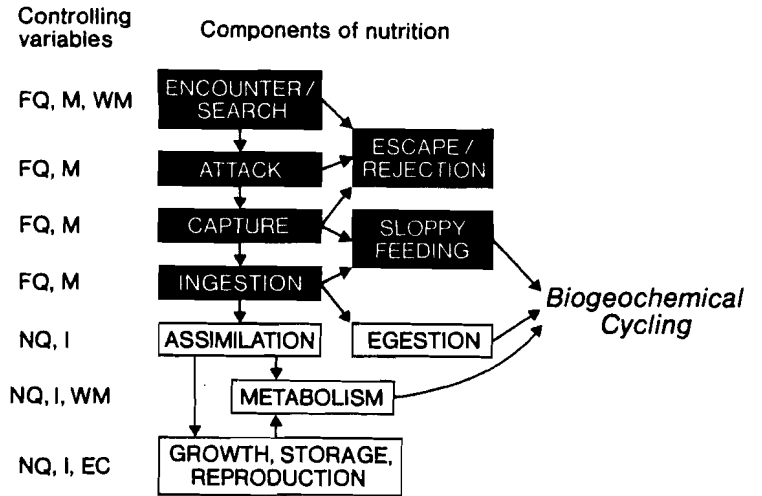
$$G_i = \psi \cdot X_i \cdot P_{E_i} \cdot P_{A_i} \cdot P_{C_i} \cdot P_{I_i} \tag{3}$$

2. The Effective Food Concentration Model

A simple mathematical model, the effective food concentration (EFC) model, encapsulates many of the main features of the components-of-nutrition framework to predict ingestion of the different particles in nature as well as quantitatively express the narratives.[30,31] Both components of nutrition and EFC frameworks will guide the discussion. The EFC model predicts the ingestion rates of different kinds of food in a mixture from knowledge of food-type (particle) concentrations (X_i) and their selectivity coefficients (W_i'). EFC is the weighted sum of the n food types, where the weighting factors are the selectivity coefficients:

$$EFC = \sum_{i=1}^{n} W_i' X_i \tag{4}$$

The selectivity coefficient is most easily determined from clearance rates (F_i) of the different kinds of foods in mixtures from the relationship $W_i' = F_i/F_{pref}$, where F_{pref} = clearance rate (units = ml per animal per day) on the preferred food. This coefficient ranges between 0 and 1 and is equivalent to the relative mortality rate coefficient (m_i) induced by the predator since m_i is proportional to F_i.[30] For a filter feeder, W_i' corresponds to filtration efficiency, assuming all particles collected are ingested. The EFC model states that the ingestion rate (G) of all foods in any mixture of foods is given by the simple functional relationship G = f(EFC), where f(EFC) may be any of the relationships used to predict the ingestion of a single kind of food, such as the Michaelis-Menton, linear, or Ivlev.[32] For example, substitution of EFC for food concentration in the Michaelis-Menton expression gives the following expression:[30]

$$G = \frac{G_{max} \cdot (EFC)}{K + EFC} \tag{5}$$

where G_{max} is the maximum ingestion rate and K is the half-saturation coefficient. The ingestion rate (G_i) on the ith kind of food is:

$$G_i = \frac{G_{max} \cdot W_i' \cdot X_i}{K + EFC}$$

(6)

G_{max} and K may be functions of environmental variables such as temperature as well as a physiological condition of the animal that, e.g., might change with feeding history and reproductive status. The basic principle of the EFC model is that Equation 4 converts the quantity of each kind of food to an equivalent amount of the most preferred food by means of the selectivity coefficient W_i'. Thus, G = f(EFC) is the same response for the most preferred food alone. Vanderploeg and Scavia[30] and Vanderploeg et al.[31] assumed that W' had to be invariant (not change) with food concentration for the EFC model to be valid. Ambler[33] showed that this assumption could be relaxed. An obvious but important corollary of the EFC model is that EFC < total particle concentration ($\sum_{i=1}^{n} X_i$). If the W' values of the different particle types are low, a suspension feeder can find itself in a high-concentration particle suspension and starve.

Clearance rates are extremely useful for understanding the interaction of the suspension feeder with its environment. We have already noted that clearance rates normalized to F_{pref} are selectivity coefficients. The clearance rate, or volume of water swept clear of particles per unit time, is the rate at which suspension feeders forage, or "search" the environment, since F has the same units as a search rate. The feeding rate (G) is the product $F_{pref} \cdot (EFC)$. Figure 4 shows the relationship of G to EFC and F_{pref} to EFC for the three commonly used models. Experimental work has shown that not all feeding relationships will fit one or any of these models, although the latter often do apply.[34,35] An important feature of all these models is that at low EFC, clearance rates are maximal (Figure 4). At low EFC, W' are often approximated from clearances rates determined for individual prey types offered singly using the same relationship $W_i' = F_i/F_{pref}$, but here the F_i = clearance rate of i is offered alone.[21] In this case, we are assuming that, like the linear model (Figure 4), the clearance rate does not change with EFC at low EFC. This also presumes that the zooplankter is in the same physiological condition in the separate experiments.

Clearance rates at low EFC represent the maximal foraging rate of the organism for a given particle type at that temperature. Therefore, it is of interest to compare weight-specific, i.e., weight-normalized, clearance rates of different suspension feeders on different particles at low concentrations to determine each one's foraging ability, because relatively low food concentrations may often be the normal situation in aquatic environments. It is also of importance to know the weight-specific G_{max}, since a high G_{max} identifies organisms adapted to high food environments or identifies opportunistic organisms adapted to take advantage of intermittent high food concentrations. In general, entire G vs. EFC and F_{pref} vs. EFC responses are of interest.

3. The Components of Selectivity Approach

W', W, and E* are generally considered to be the preferred variables for quantifying food selection, and are widely used.[4,30,36-38] I generally prefer using W' over W and E*, because W and E* values depend
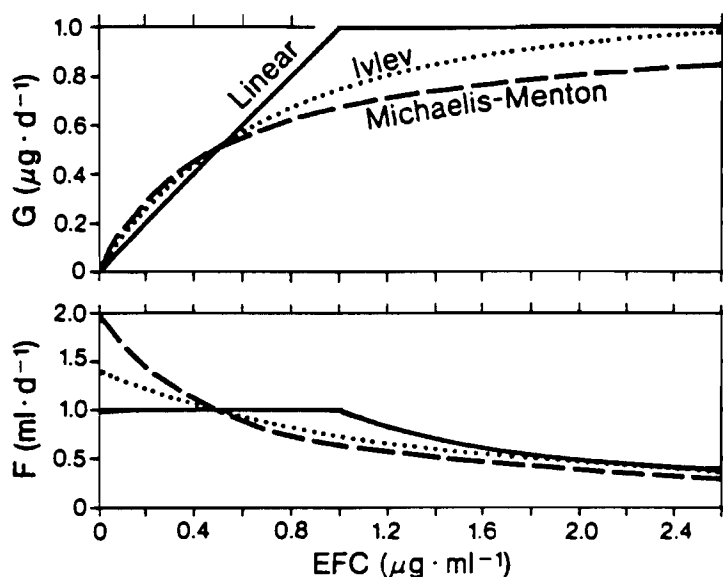
Figure 4. Theoretical ingestion rate (G) and clearance rate (F) curves as a function of effective food concentration (EFC) for linear Michaelis-Menton, and Ivlev relations. Curves were drawn so that the maximum ingestion rate (G_{max}) = 1.0 µg d⁻¹ for all relationships, and all relationships have a half-maximum G at EFC = 0.5 µg ml⁻¹. The incipient limiting concentration, the lowest EFC at which G_{max} is reached for the linear model, is 1.0 µg ml⁻¹.

on the number of prey species included, and because of the direct connection of selectivity expressed as W′ to the EFC model.[4,30,31,38] To emphasize this point, I call W′ the selectivity coefficient and W and E* electivity indices.

Another advantage of using W′ to express selectivity is that it is possible to break it down into components of selectivity in a fashion analogous to the components-of-predation approach of Holling.[29] Equation 2 may be rewritten as $G_i = \psi\, W_i'X_i$, where W_i' may be thought of as the conditional probability that the species will be ingested if it occurs in the search volume.[30,31,36,39] I say "thought of" because the prey with the highest clearance rates may not necessarily be captured if it is encountered, and because ψ can be an immeasurable quantity if we cannot specify the boundaries of the area it sweeps out. Because W′ is either this conditional probability or, in the general case, a normalized (scaled to the highest) conditional probability, we can formally break W_i' into components of predation as follows using Equation 1:

$$W_i' = P_i/P_i^* = \left(P_{E_i}' \cdot P_{A_i}' \cdot P_{C_i}' \cdot P_{I_i}' \right)\Big/P_i^* \tag{7}$$

where P_i^* is the P_i for the most preferred prey, i.e., the maximum P_i for all prey types. We take advantage of Equation 7 and speak of components of selectivity by replacing the chain of conditional probabilities with conditional selectivity coefficients:

$$W_i' = P_i/P_i^* = \left(W_{E_i}' \cdot W_{A_i}' \cdot W_{C_i}' \cdot W_{I_i}' \right)\Big/W_i^* \tag{8}$$

where W_i^* is the maximum product of the conditional selectivities in the brackets of Equation 8. Thus, we can break selection into selectivity at each stage of the feeding process. This formalism may not be used for many practical problems; however, it does emphasize the multistep process that ultimately determines selectivity. The studies of Gallager[40] on filter feeding of bivalve mollusc larvae, Williamson[41] on *Diaptomus* preying on rotifers, and Paffenhofer and Van Sant[42] on *Eucalanus* and Vanderploeg et al.[43] on *Diaptomus* feeding on particles of various food qualities are noteworthy examples of the importance of looking at the whole multistep process. The story does not quite end with ingestion since the ingested food must be digested and utilized. Therefore, it is necessary to consider the suspension feeder's ability to digest and utilize various toxic and digestion-resistant foods, e.g., toxic blue-green algae and dinoflagellates and digestion-resistant gelatinous green algae.[23] In addition, the particles not digested become egested feces (Figure 3). Thus, suspension-feeding zooplankton ingest particles of various sizes and qualities and output particles of different sizes in the form of lower-quality fecal pellets or diffuse feces, depending on the taxon. The nature of the egested material and residue left from sloppy feeding (Figure 3) has profound implications for biogeochemical cycling[23] (also see Chapter 10).

C. GOALS AND ORGANIZATION

Recently, Price[44] organized her review of the feeding mechanisms of all major taxa of zooplankton by describing the mechanisms associated with each of the steps, i.e., conditional probabilities in Equation 1. Her purpose was to do a survey of the mechanisms. My purpose is to describe selectivities and explicitly connect them to the mechanisms responsible. I am concerned about drawing generalizations about feeding types or guilds. Furthermore, the guild or feeding-type orientation is necessary because we cannot, in most cases, describe the actual mechanisms of feeding, but only how the animal functions in an operational sense. Emphasis is given to the size and quality of the selected particle, since both variables are important. Data is often presented in the format of W′ vs. equivalent spherical diameter (ESD) of the ingested particle, because ESD is a convenient way of expressing size in understandable, easily visualized units. Also, as has been done historically, ESD is on a logarithmic scale, since particle concentration in volume or mass units is roughly constant across this logarithmic scale.[45,46] For example, the upper portion of Figure 5 shows the particle-size spectra, i.e., volume of particulate material vs. ESD, in bottles of natural lake seston without and with grazing zooplankton after 1 d of feeding.[47] The lower portion shows the W′ vs. ESD curve for *Diaptomus ashlandi* determined from these data as well as W′ vs. ESD curves for *D. sicilis* and *D. oregonensis* in similar related experiments. The W′ vs. ESD curve is the selectivity-size spectrum. Our interest in particle-size spectra and grazing experiments like these can be related to the development of a Coulter counter for the rapid sizing of particles expressed as ESD and the application of this tool to marine science in the late 1960s and early 1970s.[45,46,48] It is important to recognize at the
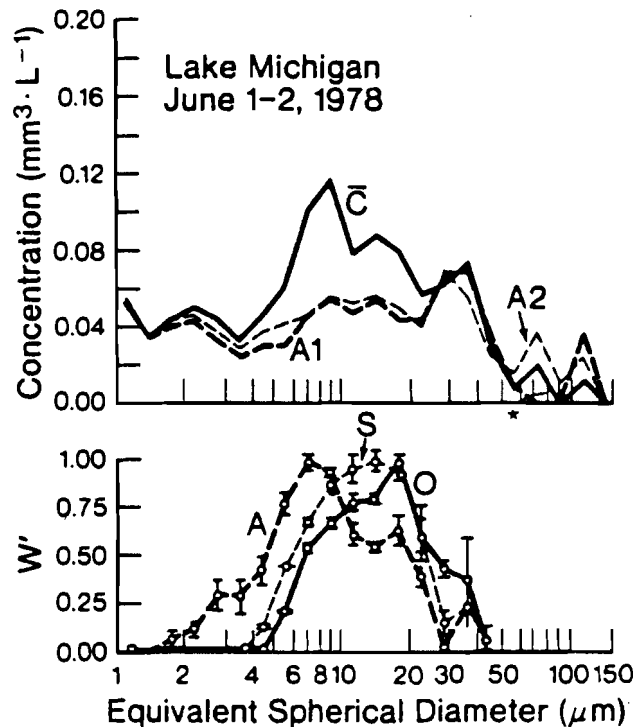
Figure 5. A feeding experiment done to determine the selectivity of *Diaptomus ashlandi, D. sicilis,* and *D. oregonensis* for natural seston in Lake Michigan. The upper panel shows mean concentration of particulate material in control containers (C̄), without zooplankton, and in experimental containers (A1 and A2), containing *D. ashlandi,* after 1 d of feeding. From the difference in these curves, the W' vs. equivalent spherical diameter (ESD) curve for *D. ashlandi* (A) was calculated. W' vs. ESD curves for *D. sicilis* (S) and *D. oregonensis* (O) in related experiments are also shown. Lengths (prosome) of *D. ashlandi, D. sicilis,* and *D. oregonensis* were 0.80, 1.2, and 1.0 mm, respectively.

outset that algae come in various shapes other than spheres (Figure 6); therefore, ESD may more or less resemble the linear dimensions of the algae.

Very often, selectivity coefficients are not available for large sets of prey types. In fact, selectivity coefficients were typically available for only pairs of prey types. To estimate W' values of large sets from smaller sets, I used the principle of maintaining proportionality between coefficients defined in smaller sets to build the larger set. An example will help (Table 1). Prey 3 is preferred to prey 2 in experiment 2, and prey 2 is preferred to prey 1 in experiment 1, as indicated by the F and W' values for the separate experiments. Clearly, prey 3 is the preferred prey; thus, we assign it an overall value of 1.0. The proportional relationship between prey 3 and prey 2 in experiment 2 is maintained by assigning prey 2 a value of 0.5. The proportional relationships between coefficients in experiment 1 is maintained by calculating an overall value of 0.25 for prey 1. This approach is most suitable for low concentrations of prey because W' does not vary with the relative proportions of prey or concentrations at low prey concentrations (as discussed below).

This chapter is mostly limited to those taxa that are suspension feeders throughout their lives and are dominant grazers in the oceans or freshwater lakes: calanoid copepods, cladocerans, rotifers, pelagic tunicates, and ciliates (Protozoa). I am using the expression "suspension feeder" in its broadest context
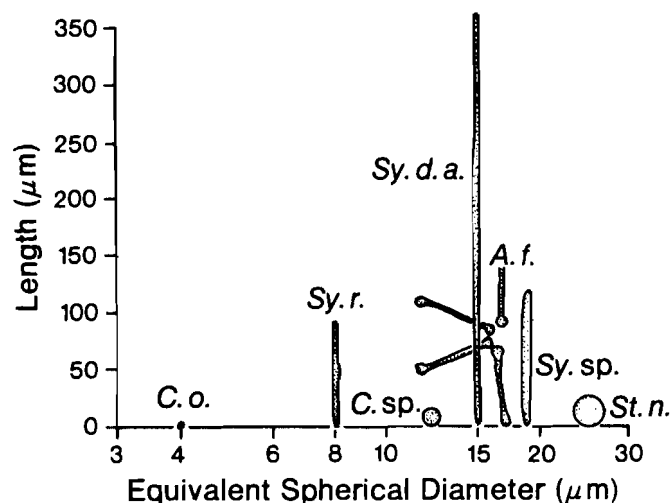
Figure 6. Dimensions of interest: lengths and equivalent spherical diameters of algae used in the study of Vanderploeg et al.[2] to evaluate effect of algal morphology in selectivity. Green algae used were *Chlamydomonas sp.* (C.sp.) and *C. oblonga* (C.o.); diatoms, shown in valve view, were *Asterionella formosa* (A.f.), *Synedra sp.* (Sy.sp.), *S. radians* (Sy.r.), *S. delicatissima* v. *angustissima* (Sy.d.a.), and *Stephanodiscus niagare* (St.n.).

to include all zooplankton that feed on small particles. Paffenhofer et al.[49] were the first that I am aware of to apply this expanded definition when they described as suspension feeders copepods that use remote detection to locate particles. Previously, the definition was synonymous with filter feeding, and copepods, themselves, were thought to be filter feeders. The suspended particles we are concerned about are in the submicrometer to approximately 200-μm size range, the

Table 1. Calculation of W' values for set of three prey from two sets of two prey each having indicated clearance rates (F) and w' values

Experiment	Prey type	F (ml d⁻¹)	W' in each experiment	Combined W'
1	1	5	0.5	0.25
	2	10	1.0	
2	2	15	0.5	0.50
	3	30	1.0	1.00

size range typically measured by the Coulter counter. By this expanded definition, some suspension feeders themselves are not much bigger than the particles they feed on, and they too would be in the size range counted by the Coulter counter. All suspension feeders discussed in this chapter, because of their small size and the relatively low current velocities they create, live in a viscous environment in which flow is laminar.

The review is not intended to be an exhaustive treatise on mechanisms, but an essay on the relationship of feeding mechanisms to feeding ecology, with emphasis on recent ideas, especially those concerned with food quality and how selectivity for different particles may change as their abundance changes. Another issue is whether zooplankton have sensory systems that can detect particles before touching them. Finally, there is the issue of how physical variables like viscosity and turbulence affect selectivity and feeding performance. I start the review with copepods because they exhibit a broad range of behaviors and mechanisms that encompass most of those of the other groups. Because of this, and the long history of study of this taxon, generalizations made here will be useful models for understanding other groups. In addition, the review is largely restricted to feeding behavior in a homogeneous environment because we do not have enough information — due to experimental difficulties — on how these suspension feeders might locate and take advantage of patches.

II. CALANOID COPEPODS: BEHAVIORALLY FLEXIBLE OMNIVORES

A. HISTORY

Much of the impetus for studying feeding mechanisms in planktonic suspension feeders can be traced to the first application of high-speed microcinematography by Strickler and colleagues in the late 1970s and early 1980s to directly observe feeding mechanisms of marine calanoid copepods.[49-51] Before these observations, herbivorous calanoid copepods were thought to be filter feeders, and selection for particles was largely thought to be a function of the size distributions of holes in the copepod's filter, the second maxillae.[52-57] Moreover, the most developed form of this model, called the leaky-sieve model, argued that the cumulative frequency distribution of holes (intersetule and intersetal spaces) in the second maxillae defined the W' curve of the copepod.[30,54,56-58] The observations of Strickler and colleagues showed that calanoid copepods created a scanning current of water that focused water near the animal's body and that the copepod responded by coordinated movements of the mouthparts to bring in a large alga it detected closer to the body and ultimately ingest it.[50,51,59,60] At the time, olfaction was hypothesized to be the stimulus for capture. Also, it was discovered that copepods preferentially ingest algae over plastic microspheres, and algal-flavored microcapsules over unflavored microcapsules.[61,62] These observations were made during a period of intense debate as to whether copepods tracked peaks in the particle-size spectrum.[3,4,61,63-66] For example, in Figure 5 this question was rephrased as: Does the peak in the W' vs. ESD curve match the peak in the particle-size spectrum (the C curve), and does the W' vs. ESD curve change from one experiment to another as the shape of the particle-size spectrum changes?[4] If the W' curve, or selectivity spectrum, does not change from experiment to experiment, this is concentration-invariant, or "invariant" selection; if it does, this is concentration-variable, or "variable", selection.[4,30,36] It was recognized that the leaky-sieve model (or passive, mechanical selection) was one way of obtaining invariant selection and, implicitly, invariant selection became equated with passive mechanical selection; therefore, the idea of invariance fell into disfavor.[4,30,31,36] The peak-tracking question is basically an

Figure 7. Slice through the flow field of *Eucalanus crassus*.[25] The slice was taken parallel to the body axis, 0 to 5 mm away from the body surface. Arrows show path lines of algae during 0- to 2-sec time intervals. Bar equals 1 mm.

optimal foraging question of whether the animal will focus its efforts on the most abundant food and thereby elevate its food intake. This question was important then, and it still motivates research. A lot of confusion in answering this invariance question arose out of three serious problems:[4,31] (1) improper methods of quantifying selection, (2) zooplankton feces production confusing what was actually ingested (i.e., particles removed), since the Coulter counter cannot distinguish between egested feces and uneaten particles, and (3) the Coulter counter does not determine the quality of the particles. The first problem was solved by the invention of W′(and W and E*), and the second and third by using methods such as microscopic counting or radiotracer methods that clearly allowed measurement of ingestion and the nature of the particles ingested. The idea of the particle-size spectrum is nevertheless useful, because size is an important variable. We can start examining this problem by looking at mechanisms responsible for the selection of high-quality food of different sizes.

B. SELECTIVITY, FEEDING RATES, AND MECHANISMS
1. Selection of High Quality Food

A great many copepods, especially those with strong herbivorous tendencies, move very slowly and create a strong double shear current (focused flow in both lateral and vertical directions from the body axis) in which they detect and capture particles. Figure 7 shows a slice through the flow field around a free-swimming *Eucalamus crassus*, a marine calanoid copepod that creates such a scanning current. Figure 8 shows different theoretical cores or regions of particle capture for *E. crassus*.[25] Any particle within the motion or viscous cores automatically travels to the mouthparts in the capture area. The motion core is just the forward projection of the capture area, and the viscous core represents the region of the
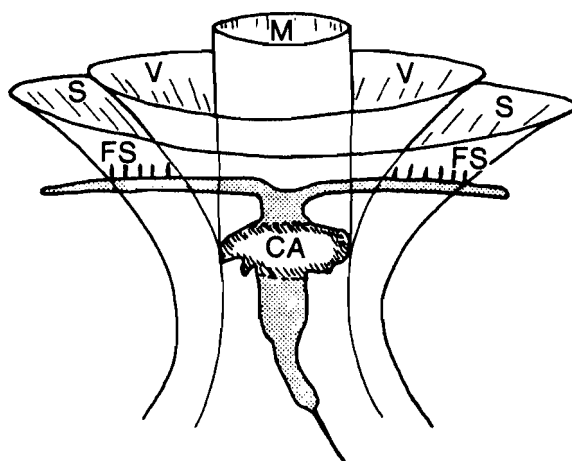
Figure 8. Diagram explaining the terms motion core (M), viscous core (V), and sensory core (S).[25] CA, capture area; FS, sensory fields on first antennae.

Figure 9. Lateral views of the anterior portion of the bodies of copepods studied by high-speed microcinematography. Figures were redrawn from Koehl and Strickler,[51] Vanderploeg and Paffenhofer,[67] and Paffenhofer and Stearns.[35] The appendages labeled are: first antenna (A1), second antenna (A2), mandibular palp (MP), first maxilla (M1), second maxilla (M2), maxilliped (MXP), and swimming feet (S).

Eucalanus pileatus

Diaptomus sicilis

Acartia tonsa

Paracalanus sp.

double-shear current field outside of the motion core that leads to the capture area. The sensory core represents that region outside of the viscous core in which particles can be detected, presumably by the sensory fields on the first antennae. To capture particles in the sensory core, the zooplankton must actively move toward the detected particle. The resulting capture is described as an active capture. Most o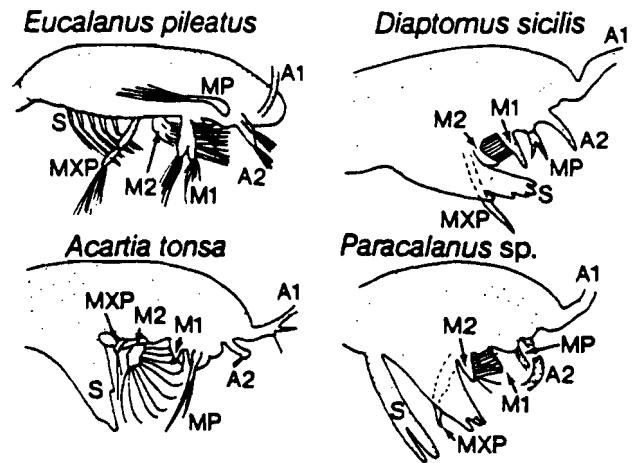f the discussion focuses on *Diaptomus*, because it is one of the four copepods intensively studied by high-speed microcinematography (Figure 9) and because selectivity and feeding rate have been explicitly related to feeding mechanisms in this species.[2,31,35,51,67,68] The W' vs. ESD for *Diaptomus* is shown for easily ingested, high-quality algae and an easily ingested, soft-bodied, slowly-moving rotifer in Figure 10. Selectivity increases with the increasing size of the alga or rotifer. For comparison, the W'' curve predicted from the leaky-sieve model is shown.[58] Clearly, the leaky-sieve model is a poor predictor of the empirically determined W' curve shown in Figure 10. Above the monotonically increasing W' vs. ESD curve are shown the capture modes used to capture the particles. Very small particles are captured passively without detection by the copepod. The passively captured small particles carried in the motion or viscous cores flow in undetected between the paired second maxillae or between the spaces between setae (the projections on M2 in Figure 9) and are funneled toward the mouth.[67,69] Theoretically speaking, this is interesting because calculated boundary layer thicknesses around the setae should prevent particles from flowing between the setae under these conditions of laminar flow.[69]

As particles get larger, an increasing proportion of them are captured actively, i.e., they are detected in the laminar double-shear scanning current, and coordinated motions of the mouthparts are used to bring the particles between the second maxillae. The fling and clap motion described by Koehl and Strickler[51] is used to squeeze out the water to get the particles between the second maxillae. As algal size gets larger and larger, a greater proportion is captured actively, and the larger particles are detected at a greater distance.[67,70] For example, in the case of *D. sicilis*, the fling and clap motion of the second maxillae (M2

Figure 10. The W' vs. equivalent spherical diameter (ESD) curve for *Diaptomus* feeding on high-quality food (solid line). This curve is a composite of results from experiments of Vanderploeg et al.[2] for *D. sicilis* feeding on the algae *Chlamydomonas* sp., *C. oblonga*, *Stephanodiscus niagare*, and *Synedra* sp., as well as results from Williamson and Vanderploeg[68] for *D. pallidus* feeding on the rotifer *Synchaeta oblonga*. For comparison, the prediction of the leaky-sieve model is shown. Capture modes for the particles are shown above the curves.

Capture Mode

Active

Thrust

Passive

Leaky-Sieve Model

W'

ESD (μm)
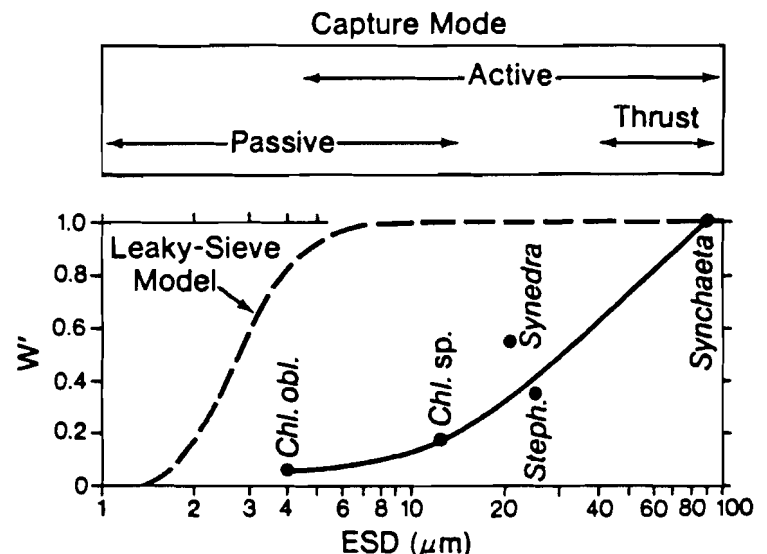
in Figure 9) is used to capture algae nearby and the maxillipeds (MXP in Figure 9) help capture particles at greater distances from the body. The proportion of maxilliped-aided capture increases with algal size. Thus, there is a perceptual bias for large algae. These observations require a minor modification of the sensory core hypothesis. As particles get larger, the perception core increases, and it may be more appropriate to think in probabilistic terms: larger particles in a given region have a larger probability of detection than smaller particles.

Synchaeta, the most preferred of all *Diaptomus'* prey, was captured actively like the algae or with a thrust response that has only been observed for the capture of microzooplankton. The thrust response involves a sweeping back of the first antennae (A1 in Figure 9) and a vigorous thrust of the swimming feet (S in Figure 9) to pounce on the prey. This vigorous thrust is probably not just an enthusiastic response to a distantly perceived large particle, but probably represents a directed attack toward a target that *Diaptomus* recognizes as animal prey.[68] Such a directed attack is necessary for capturing microzooplankton, since many microzooplankton detect the copepod's scanning current and have well-developed escape capabilities.[68]

2. Effect of Food Quality

Food quality is an important controlling variable (Figure 3) that appears at each component of predation. Typically, food quality of a particle is regarded as its nutritional content for the predator. For example, a nutritious particle would be one that was nontoxic, digestible, and contained a balanced composition of proteins, lipids, carbohydrates, and micronutrients to allow growth and reproduction of the suspension feeder. Along with nutritional quality, it is necessary to include any factors that would diminish the suspension feeder's ability to detect, capture, and ingest a particle. These nonnutritional factors would include, for example: size and other qualities as they affect detection or filtering efficiency, size and shape as they affect handling and ingestion, and escape abilities of motile prey. For copepods, both nutritional and nonnutritional factors are reflected in the selectivity coefficients.

a. Nutritional Quality

Thus far, we have argued there is a perceptual bias for the capture of large algae and microplankton. Olfaction of the alga was hypothesized by Strickler and colleagues to be the cue used by the copepods.[50,51,59,60,71] According to this view, expressed in the mathematical model of Andrews,[71] the calanoid copepod creates a laminar double-shear scanning current, and the phycosphere of algal exudates becomes elongated in this field to form an active space that arrives at the copepod's chemosensors on the antennae while the alga is in the sensory core in front of, or near, the antennae.[71] Olfaction is not the only mode of distance perception of nonmotile algae and other particles: the high-speed motion pictures of Vanderploeg et al.[43] showed that *Diaptomus* routinely actively captured large inert plastic microspheres (>14 µm). These results argue that physical cues alone may be sufficient for eliciting active capture of large particles, but possibly not smaller particles. The details of how this combination of physical and chemical cues is used need to be worked out.

Indirect support for mechanoreception comes from DeMott and Watson's experiment[72] showing the clearance rate and selectivities of *D. birgei* for *Chlamydomonas reinhardti* (~5 µm ESD) and *Pediastrum* (80 × 80 µm) were unaffected by the presence of high concentrations of sugars, amino acids, and algal extracts which they believed should have obscured the phycosphere of odor around the algae. In this same study, they showed that the *Diaptomus* clearance rate was unaffected by algal motility, whereas motility greatly increases the clearance rate for the cyclopoid copepod *Tropocyclops*. Cyclopoids, which are typically predators and do not create scanning currents, respond to prey movement. These observations supporting the role of mechanoreception are consistent with the recent observations of Yen et al.[73] showing that the mechanoreceptors on the first antennae of copepods are sensitive to small displacements over a wide frequency range. It will be interesting to learn how the mechanoreceptors perform on copepods that create scanning currents and on those that depend on prey movement for detection.

Thus, biochemical or nutritional quality affects perception of a particle by the cloud of exudates around it. Biochemical composition also affects selectivity after capture of the particle because contact chemoreceptors near the mouth are used to taste the particle before ingestion.[74] Observations of the rejection process give clues to how this taste process operates. Large algae or particles like fecal pellets are usually ingested or rejected very soon after being brought to the mouth, whereas small algae or plastic microspheres captured passively are ingested or rejected as a group after several have accumulated near the mouth.[42,43,67,75] Small particles of low nutritional quality can be hidden among a larger mass of high-quality food and be ingested.[42]

Table 2. **W′ of eucalanus pileatus for particles of different equivalent spherical diameters (ESD) and nutritional quality**[66]

Particle	ESD (μm)	Active capture (%)	W′ Offered alone	W′ Offered in pairs
Rhizosolenia alata (live)	59	~100	1.0	1.0
R. alata (dead, heat killed)	59	—	0.63	0.83
Thalassiosira weissfloggi (live)	14	63	0.36	0.30
Fecal pellets	51	66	0.43	0.44
Polystyrene spheres	20	7	0	0.02

The combination of physical and olfactory cues for distance perception and taste before ingestion implies that the copepod has a sophisticated two-step process that encourages ingestion of large, high-quality food. At first glance, this capture of large inert particles would seem maladaptive; however, there are few large inert particles (minerals, sediments, or refractory detritus) in open lake or marine environments.[26,27,43] These big particles could be fecal material whose scent is disguised by an enclosing (periotrophic) membrane (see below) or could be microzooplankton that would escape if Diaptomus delayed while obtaining or processing a chemical signal.[43] The sensitivity and possible operation of this two-step system can be appreciated from a closer look at Paffenhofer and Van Sant's[42] results (Table 2). The dead Rhizosolenia alata and fecal pellets, both about the same size as live R. alata, were captured at lower rates. The fecal pellets had a selectivity about the same as the small alga, Thalassiosira weissflogii. Also, the percentage of captures that were active captures for pellets and T. weissflogii were 66 and 63, values less than the ~100% observed for R. alata. The lower active-capture proportion for fecal pellets may be caused by a smaller olfactory cue arising from it or possibly its smaller size, particularly length (see below).

Both lack of active captures and postcapture rejection were responsible for the complete lack of ingestion of 20-μm microspheres offered alone in the experiments of Paffenhofer and Van Sant.[42] Very few microspheres were captured, and only 1 of 15 observed captures was apparently an active capture. Lack of active captures is not surprising, since a 20-μm microsphere is small relative to the large size of Eucalanus. None of the captured microspheres were ingested. In a mixture of T. weissflogii and microspheres, 42% of the captured microsphere were ingested. Thus, inert particles are passively captured and ingested incidentally with the algae. This explains the low, but nonzero, W′ for beads in Table 2.

Other studies of the effect of nutritional quality parallel those of Paffenhofer and Van Sant.[42] In their tabulation of previous work, Paffenhofer and Van Sant noted that W′ for dead algae was between 0.52 and 0.90 relative to that of live algae, with a mean of 0.63; W′ for fecal pellets was 0.43 to 0.90 relative to living algae. DeMott[76] also showed that dead algae were less preferred than live algae; however, in addition, he showed that colonization of the dead algae by bacteria improved selectivity. Cowles et al.[77] and Butler et al.[78] showed that copepods preferentially select rapidly growing, N-sufficient algae over slowly growing, N-deficient algae.

Selection for algae of different species varies with nutritional quality. The results of DeMott[76] with Eudiaptomus (a close relative of Diaptomus sicilis) show that algae with gelatinous sheaths, which may inhibit digestion, have lower selectivities than high-quality algae (Table 3). As can be seen in Table 3, selectivity for toxic blue-green algae is very low. Similar results were reported by Fulton[79] and Vanderploeg et al.[43] Vanderploeg et al.[43] showed that toxic blue-green algae filaments are readily captured actively, but that they are almost always rejected after they are brought to the mouth. Presumably, the toxic substance or some associated chemical is the "taste" responsible for rejection. Marine calanoid copepods do not appear to be able to taste prior to ingestion toxins associated with toxic dinoflagellates, the major group of toxic algae in the oceans, since the rejection mechanism appears to be regurgitation, and the feeding rate on both toxic and nontoxic algae in mixtures is reduced drastically.[80]

Possibly both taste and perceptual bias play a role in the lower selectivity of the large (23 μm) gelatinous alga Planktophaeria compared with Chlamydomonas (Table 3). The gelatinous sheath, which protects at least some species of green algae from digestion,[81] may inhibit ingestion since, once captured, the sheath may inhibit the taste from coming through, or possibly the sheath itself may not have a good taste. Notice in Table 3 that selectivity for the gelatinous alga decreased at high algal concentration.

Table 3. Selectivity (W') of *Eudiaptomus* for the less preferred alga in indicated pairs of algae of different food quality (H = high, T = toxic, G = gelatinous sheath) offered at high and low food concentrations[76]

Food pair	ESD (μm)	Food quality	Alone	W' Low	W' High
1. *Scenedesmus*	5	H	0.67	0.79	0.72
Chlamydomonas	12	H			
2. *Microcystis*	5	T	0.060	0.18	0.15
Monoraphidium	3.5	H			
3. *Planktosphaeria*	23	G	0.82	0.54	0.16
Chlamydomonas	12	H			

Note: W' is given only for the less preferred alga in the pair; by definition, W' of preferred alga = 1. Concentrations of each alga offered alone or in pairs at the low concentration were each 0.125 mm^3 l^{-1}. The concentration of algae offered in pairs at the high concentration were each 1.0 mm^3 l^{-1}.

DeMott[76] described this concentration-variable selectivity as an optimal-foraging strategy. This issue is discussed below.

DeMott[82,83] used microspheres flavored by algal exudate, after the technique of Rassoulzadegan et al.,[84] as a tool to evaluate and classify the selective abilities of different zooplankton taxa by offering them mixtures of unflavored microspheres, microspheres flavored with algal exudate (by soaking them for ~1 d in a high concentration of algae), and the algae themselves. If taste is not a factor in food selection, then algae and flavored and unflavored microspheres of the same size would have the same selectivities. These experiments are relevant, first, because of the potential power of the technique to rapidly classify the different species' selective abilities by adding microspheres and algae to bottles of water containing the natural assemblage of zooplankton. Second, flavored microspheres may represent an analog of suspended or resuspended mineral particles in nature more closely than do unflavored microspheres. These particles may pick up algal exudates in the water column or when they reside on the lake bottom or seafloor before resuspension.

Table 4, calculated from results of DeMott,[83] shows the following order of selectivity: *C. reinhardti* (ESD = 6 μm) ≫ flavored microspheres ≫ unflavored microspheres. In addition, there is a preference for small microspheres to large microspheres: flavored 6-μm microspheres were preferred to 12-μm flavored microspheres, and unflavored 6-μm microspheres were preferred over unflavored 12-μm microspheres. The cinematographic observations of Paffenhofer and Van Sant[42] and Vanderploeg et al.[43] reveal the mechanisms behind these results. Vanderploeg et al.[43] showed that unflavored 11-μm microspheres are captured passively like most of the 6-μm *C. reinhardti*. Small microspheres are less likely to be rejected because they can hide among an accumulated mass of *Chlamydomonas* and not be detected as low-quality food, whereas a captured large microsphere or microspheres are more likely to be detected as low-quality food. Recently, Bern[85] showed that *Eudiaptomus* did not strongly select 6-μm algae over 6-μm microspheres in experiments in which the beads and algae were introduced into the natural seston of an eutrophic lake. Perhaps the microspheres were hidden among numerous particles of lake seston that formed the mass of particles to be ingested or rejected after tasting. Perhaps the natural seston as a group had a lower food quality than the labeled algae, and the copepods were acclimated to a lesser taste-signal strength to induce the ingestion response. The message that should be clear from all the work reviewed here is that whether a microsphere or inert particle is ingested depends on its size and what other particles are available.

b. Size, Shape, and Motility

As seen in Figure 10, there is a perceptual bias for larger targets. The physical shape of the target may affect the copepod's ability to detect an alga. Notice that the W' of *Synedra* in Figure 10 is larger than that of *Stephanodiscus*, which has a larger ESD. *Stephanodiscus* is a pill-shaped diatom whose width and height are about the same as its ESD (Figure 6), whereas the elongated *Synedra*, with an ESD of 21 μm, has a length of 125 μm. Vanderploeg et al.[2] hypothesized that rotation of (randomly oriented) elongated algae, as they become aligned in the double-shear scanning current of the copepod, creates a noise that the copepod could respond to. Ultimately, as seen in Figure 5, as particle size increases relative to the

copepod, it becomes too large for ingestion. Round algae may become too large to fit in the mouth, and algal colonies elongated in two dimensions — like the stellate colonies of *Asterionella* (Figure 6) — cannot be handled for ingestion if their dimensions are greater than those of the mouthparts used to handle them.[2] Copepods can ingest very long algal cells (e.g., *Synedra delicatissima* v. *angustissima* in Figure 6) and filaments (of the order of millimeters) by orienting the filament perpendicular to the body axis and the pushing it into the mouth.[2,49]

Rotifers use morphological and escape tactics to foil predation by *Diaptomus*.[41,68] *Synchaeta*, the most preferred prey of *Diaptomus* (Figure 10), is a slowly moving, soft-bodied rotifer without effective defense mechanisms. The highly palatable soft-bodied *Polyarthra* escapes ingestion by being able to sense the current field of *Diaptomus* and then tumble away quickly (280 body lengths per second) using its four

Table 4. W' relative to *Chlamydomonas reinhardti* of *Eudiaptomus* for unflavored microspheres and microspheres flavored with exudate of *C. reinhardti*[73]

Flavoring	Diameter (μm)	W'
Flavored	6	0.19
Unflavored	6	0.025
Flavored	12	0.071
Unflavored	12	0.0061

Note: Microspheres were flavored by soaking them in a suspension of 5×10^5 cells per milliliter for ~1 d. Results are for mixture experiments with a low concentration (1000 cells per milliliter) of algae. Percent standard errors of the mean for all W' data are, approximately 25%.

triplets of paddles. *Keratella* exhibits no escape response to *Diaptomus*, but once captured it is manipulated, pressed up against the mandibles, and ultimately rejected. The hard lorica (body surface) and spine of *Keratella* probably foils ingestion.

3. Concentration-Variable Selectivity and Motivation

There has been much interest in the question of concentration-variable selectivity because it may imply an optimal foraging strategy to maximize consumption of an abundant high-quality or easily handled food. Vanderploeg et al.[2,43] demonstrated that W' of *Diaptomus* for a small (4 μm) species of *Chlamydomonas*, which is captured passively, remained constant at about 0.3 relative to a large (12 μm) species of *Chlamydomonas*, which can be actively captured, over a broad range of concentrations with different ratios of the two species. Both Paffenhofer[86] and Vanderploeg et al.[2] showed that selectivity of elongated algae, which must go through a complicated handling sequence before ingestion, drops at high algal concentrations. The data of DeMott[76] for "low quality" *Planktosphaeria* (Table 3), as well as other algae, show a similar pattern.

These drops in selectivity suggest optimal foraging because selectivity for the "less desirable" alga drops at high food concentrations; however, Vanderploeg et al.[2,43] argue that it does not conform to optimal foraging in that selectivity for the less desirable alga drops as its concentration is increased relative to the high-quality or easily handled food. Vanderploeg et al.[2,43] argue that this is a satiation-driven behavior that results from the organism being placed in a food-rich environment for which it was not designed. In these high-concentration situations, *Diaptomus* continues to actively and passively capture algae and then reject much of what it has captured. Thus, the broad pattern of lower selectivity for the less-desired particle conforms to optimal foraging; however, it occurs while the organism is behaving in a nonoptimal way of catching and throwing away captured particles of high nutritional value. Vanderploeg et al.[2,43] note that these behaviors can be explained by simple behavioral (ethological) mechanisms affected by motivation. We cannot expect organisms to behave optimally in all situations, since optimality must operate through sensory and motor pathways that are not infinitely flexible but have certain rules of their own. Moreover, selection pressures also constrain the organism to a certain region where it can operate in an efficient way. Finding these behavioral rules is more likely to lead to models of greater generality and accuracy than optimal foraging narratives that we articulate *a priori*. Studying these mechanisms may also lead to new, unsuspected optimality principles. No concentration-variable selectivity has ever been reported for low algal concentrations; however, this is not to say that this phenomenon does not occur in certain species. Such a possibility is suggested by Price and Paffenhofer's[87] observation that *Eucalanus* initiated second maxillae vibration to enhance the capture of small cells when they became abundant.

Motivation is indicated as an important controlling variable for each component of predation (Figure 3). Obviously, as discussed above, hunger is an important form of motivation that affects each component. Another form of motivation is escape from predation. Zooplankton vertical migration is often a

response to avoid predation.[88] Food-rich areas may be avoided if predators are present. In addition to this obvious response, the swimming behavior of zooplankton may change in the presence of predators. *D. tyrelli* cruises less and suffers a lowered feeding rate in the presence of exudates from the predacious calanoid copepod *Epischura nevadensis*.[89] *D. sicilis*, which coexists in the hypolimnion with the predacious calanoid copepod *Limnocalanus macrurus*, swims more quietly (jumps less) in the presence of this predator.[90] It is not known whether these changes in swimming patterns have any effect on selectivity.

4. The Generic Calanoid Copepod

For a long while we have believed in the idea of a single generic calanoid copepod. That is, if we understand *Diaptomus* or *Eucalanus*, we understand all copepods. Strickler,[25] based on cinematographic observations of two different species of *Eucalanus*, challenged this assumption by putting forth two important hypotheses: (1) calanoid copepods produce species-specific and, perhaps, age (stage)-specific feeding currents and (2) ambient water motions (turbulence) act as a mechanism for niche separation of calanoid copepods. Recent experimentation has generally validated these hypotheses. Cinematographic observations have shown that there are significant differences in mouthpart use and feeding currents even among those species that have been regarded as omnivores with strong herbivorous tendencies, namely, *Diaptomus, Eucalanus, Paracalanus,* and *Acartia* (Figure 9). It is worth noting that probably no calanoid copepod is strictly herbivorous. *D. minutus*, one of the smallest if not the smallest freshwater calanoid, prefers cilates to small and medium-sized algae.[91] *Diaptomus, Eucalanus,* and *Paracalanus* are alike in that they use their mouthparts, including the maxillipeds, to create a double-shear scanning current.[91] In contrast, *Acartia* (Figure 9) has reduced maxillipeds and does not create a scanning current, but instead uses seining motions of its second maxillae to capture prey[35]. In estuaries, where *Acartia* lives, a scanning current could be less useful for locating the prey because the turbulence typically found there could disrupt the scanning current.[35] This seining is effective in the food-rich environment of the estuary but not in offshore waters, where food concentration is low.[35] Also, *Acartia* typically spends much time sinking.[92] During sinking, *Acartia* detects moving prey without signaling its presence.

Paracalanus and *Diaptomus* look very similar, use their appendages the same way, and probably have very similar selectivity patterns, although it has not been documented that *Paracalanus* can capture microzooplankton.[2,35,67] The lack of well-developed swimming feet (thoracopods) on *Eucalanus* may imply that it is not adapted to capture microzooplankton. Very predacious copepods cruise rather than scan, and they use mechanoreception to detect motile prey.[59,93-95] The different feeding mechanisms can be correlated with different feeding rate vs. food concentration curves. For example, *Acartia* exhibits threshold feeding behavior, i.e., the clearance rate drops to low levels at low particle concentrations.[35] This response may be an appropriate energy-conserving mechanism for its feeding method and environment.[35] Thus, there is more than one generic copepod. The degrees to which chemoreception and mechanoreception play important roles need to be worked out for more species. The work to date serves as a foundation on which to build.

Related to the generic copepod problem is that caused by life stage: copepods go through six naupliar and five copepodite stages before becoming adults. Most work on feeding and its mechanisms has focused on adult females, as I have done in this chapter. Morphology, appendage use, and feeding mechanisms vary with the stage of the copepod, as Strickler[25] recognized in his first hypothesis. For example, nauplii create a feeding current and capture large cells actively. They cannot capture cells passively because they do not have the appendages to do this. As a result nauplii, relative to their size, capture large particles, even elongated (500 μm) algae like *Rhizosolenia*.[96] The ontogeny of appendage use, sensory mechanisms, and behavior is an area deserving further study, especially in view of the abundance and grazing impact of the juvenile stages.[96]

5. Turbulence and Components of Nutrition

Turbulence is listed as a controlling variable for two components of nutrition: encounter/search and metabolism. Modeling studies[97-99] and experimental work with *Centropages hamatus* and *Acartia* have shown that the encounter rate with prey is increased under turbulent conditions.[10,12,24] The feeding rates of *Acartia* on algae increased at "moderate" levels of turbulence, and decreased at high levels, presumably because of disruption of feeding currents,[13] as hypothesized by Strickler.[25] The rate of egg cannabalism of *Acartia* in a study by Saiz et al.[13] was depressed more than the feeding rate of algae under turbulent conditions. Saiz et al.[13] argued that this may have been a result of distance mechanoreception of the eggs being disrupted by the turbulence. This, then, may be taken as evidence for turbulence affecting

selectivity. No study to date has examined a copepod like *Diaptomus*[67] or *Temora*[92] that spends most of its time creating a scanning current. Nutrient excretion in *Acartia* was also increased under turbulent conditions,[100] probably in response to increased metabolic rate associated with more frequent escape responses.[24]

III. CILIATES AND ROTIFERS: DIVERSE GENERALISTS AND SPECIALISTS

A. INTERESTING ANALOGIES

Although ciliates — found in both marine and fresh waters — are protozoans, and rotifers — found primarily in fresh water — are metazoans, I discuss these taxa together because many of them have analogous feeding strategies, and we could put some species from each taxon in the same feeding guilds. Both taxa are small, ciliates typically 20 to 100 μm long and rotifers typically 100 to 500 μm. Both taxa include species exhibiting polyphagy and extreme stenophagy. Not only may they feed on the same food, they also (as recent work shows) are favored prey of freshwater and marine calanoid copepods.[101,102]

B. CILIATES
1. Filter-Feeding Ciliates

Fenchel[103] reviewed the possible mechanisms of suspension feeding — inertial forces, diffusion, gravity, direct interception (=raptorial feeding in the sense, he thought, that ciliates bumped into food), and sieving — by ciliates and concluded that sieving and raptorial feeding were the major mechanisms.[104] He gave a detailed account of the hydrodynamics of the filter feeding of different groups of ciliates. The size of particles collected by the ciliary filter is closely correlated with the spacing between cilia, and the ciliate has little capacity to select particles of different nutritional quality. Many filter-feeding ciliates are adapted for feeding on bacteria and other picoplankton (<2 μm). The broad principles of his analyses of feeding mechanisms will probably remain intact, although recent work has questioned certain details. Sanders[105] showed that surface effects (charge) can affect the accumulation of large bacteria-sized (0.9-μm) particles, but not small (0.6-μm) particles. Monger and Landry[106] have argued that the geometric model of Fenchel[103] must be modified to include surface interactive forces at least when used to describe the feeding of very small protozoans.

Fenchel[103] showed that ciliates having greater distances between cilia generally have higher clearance rates, and that bactivorous ciliates, which must have very small spacing between cilia to capture bacteria, are usually found only in eutrophic environments where food concentrations are high enough to compensate for their lower clearance rates. Water transport to the ciliate is assumed to be independent of particle concentration, and the maximum feeding rate is limited by the food vacuole formation rate.[103,107] The ingestion rate follows Michaelis-Menton kinetics.[107] Since food vacuole formation is less efficient for large particles, the maximum feeding rate is affected by the proportion of large particles in the mixture.

2. Raptorial Ciliates

The raptorial ciliates feed on algae and other microzooplankton and are often specialists on particular organisms.[108-111] The raptorial ciliates prefer large particles. Tintinnids ingest particles that are up to 45% of their body diameter, and oligotrichs commonly ingest algae almost as large and even larger than themselves.[112-116] I am concerned with the phytophagous taxa because they are important grazers in waters of varying trophy in both marine and fresh water.[108,117,118] For example, in both the eutrophic and oligotrophic Great Lakes, ciliate biomass rivals crustacean biomass.[117,118] Given their high respiratory demands, the ciliate grazing impact should be greater than that of crustacean zooplankton.

The phytophagous ciliates can be highly selective. *Favella ehrenbergii* requires dinoflagellates for growth, and only small amounts of other algae in the proper size range are consumed.[108] Chemical cues were suggested as the mechanism for selection because dinoflagellates, regardless of type of body wall, were ingested. Freshwater *Coleps* can survive only on flagellates.[109] *Nassula* is specialized to feed on filamentous blue-green algae and will not feed on green algae, diatoms, or nonfilamentous blue-green algae.[110] *Nassula* uses its specialized cytopharyngeal basket to grasp, fold in half, and coil the filament into its body.[119]

It is possible that ciliates must ingest particular algae because of certain specific biochemical requirements, digestibilities, and factors associated with handling. It is also possible that certain algae, like the dinoflagellates in the *Favella* example, have exudates that act as very specific chemical signals to the
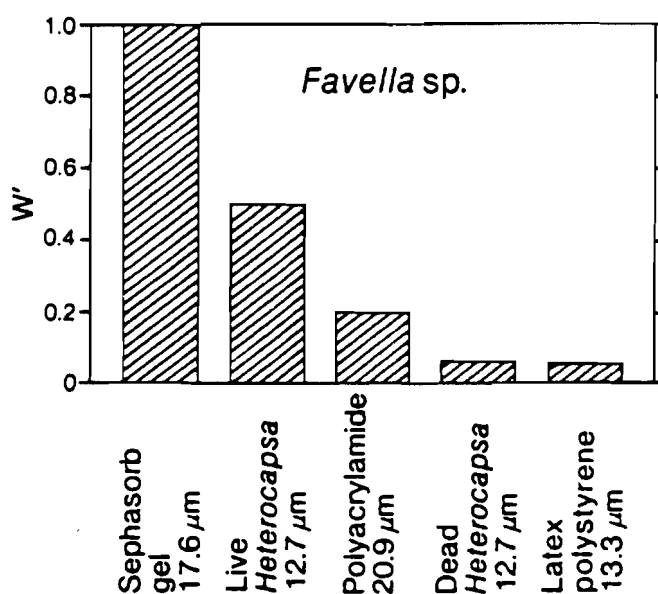
Figure 11. Selectivity (W′) of the ciliate *Favella* sp. for different particles in the experiments of Stoecker.[116] This set of W′ values was deduced from her sets of paired experiments.

ciliate. This latter possibility is strongly suggested by Taniguchi and Takeda,[120] who observed with high-speed videography that the capture response to a favored food was initiated before the food made contact with the oral membrane of the ciliate. Likewise, unfavorable foods were rejected before or at contact with the oral membrane. Unfavored cells, which were accidentally captured, were rejected from the peristomal cavity.

The selection process in ciliates is far from understood. A curious example is the selective feeding of *Favella* sp. in paired mixtures of live algae, dead algae, and microspheres of various kinds.[116] The results of these paired experiments were combined to give the overall W′ result in Figure 11. Certain microspheres were preferred even over live algae. Live algae were preferred to dead algae and other types of microspheres. Surface properties, either chemical or physical (charge, for example), must be responsible for this result.

The only experiment to see if the selectivity of a ciliate changes with the relative concentration of food was done with *Balanion* sp. feeding on a mixture of the dinoflagellate *Heterocapsa* and the green alga *Dunaliella*.[121] The results of this experiment are redrawn and analyzed in Figure 12, because their form of presentation gave the impression of variable selectivity. Data were presented as the proportion (r) of *Heterocapsa* in the diet as a function of the proportion (p) available. If selection for each algal species were the same, then the data points would fall on the straight line labeled $W_H' = W_D' = 1$. The r values fell to the upper left, indicating a strong preference for *Heterocapsa*. The variable r values do not imply variable selectivity, because the curved line predicted by a constant W′ value of 0.05 for *Dunaliella* fit the r vs. p data very well.

C. ROTIFERS: GENERALISTS AND SPECIALISTS

The feeding habits of rotifers are related to the morphology of the ciliary corona, which produces the feeding current, and the mastax, which grasps and in some cases grinds the food before swallowing.[122] Little is known about the hydrodynamics of swimming and feeding or the function of the feeding organs, because high-speed cinematography or videography, which is necessary for observation, has not often been applied.[123] Gilbert and Bogdan[124] classified rotifers as generalists or specialists depending on the functional morphology of the coronae. The selectivities of generalist and specialist rotifers shown in Figure 13 were calculated from raw data on filtering rates in their experiments. The presentation of results is very similar to theirs, except that W′ is used instead of the selectivity index D. The generalists — *Keratella*, *Conochilus*, and *Kellicottia* — have a bell-shaped W′ vs. ESD curve, showing preference for intermediate-sized particles. *Polyarthra*, a specialist, showed preference for flagellated algae, especially *Cryptomonas*. The specialist *Synchaeta* strongly specialized on *Cryptomonas* and preferred *C. erosa*, the larger of two species on which it was cultured. All the generalists have extensive, finely ciliated buccal fields in which a wide variety of particles may be transported to the mouth. The coronae of the specialist rotifers are more sparsely ciliated. They seem designed for capture of individual particles. Presumably

Balanion

Figure 12. Proportion (r) of the dinoflagellate *Heterocapsa* in the diet of the ciliate *Balanion* sp. as a function of proportion of *Heterocapsa* available in mixtures of *Heterocapsa* and an alternate prey, the green alga *Dunaliella*. Results from Stoecker et al.[121] redrawn with the r curve predicted from W' of *Dunaliella* equal to a constant value of 0.05. The line $W_H' = W_D' = 1$ is the line along which all data would fall if W' values of both algae were equal.
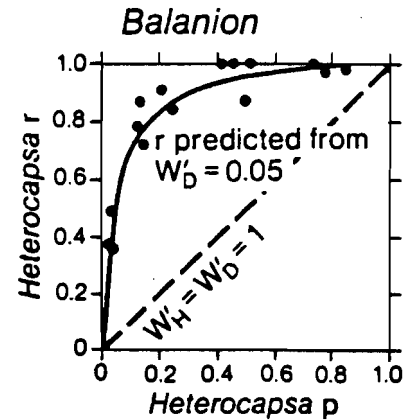
these specialists, like the raptorial ciliates, detect their prey before or at contact by physical or chemical means.

Other rotifers exhibit stenophagy.[122] One of the more interesting examples is *Notholca squamula*, whose abundance is closely correlated with that of the diatom *Asterionella formosa*.[125] This 120-μm-long rotifer feeds by biting the ends off the cells (~75 μm long) in the stellate colonies (diameter ≃ 150 μm, Figure 6) with a strong crushing action of its well-developed trophi. Remember, the stellate colonies of *Asterionella* offered protection against grazing by *Diaptomus*. Algae other than *Asterionella* were rejected by *Notholca*. This selection and the close coupling of *Notholca* abundance to that of its prey, which is reminiscent of the ciliate/dinoflagellate coupling, suggest that *Notholca* is keying in on very specific chemical information to make its choice of prey.

Keratella, Conochilus, Kellicottia

Polyarthra

Synchaeta pectinata
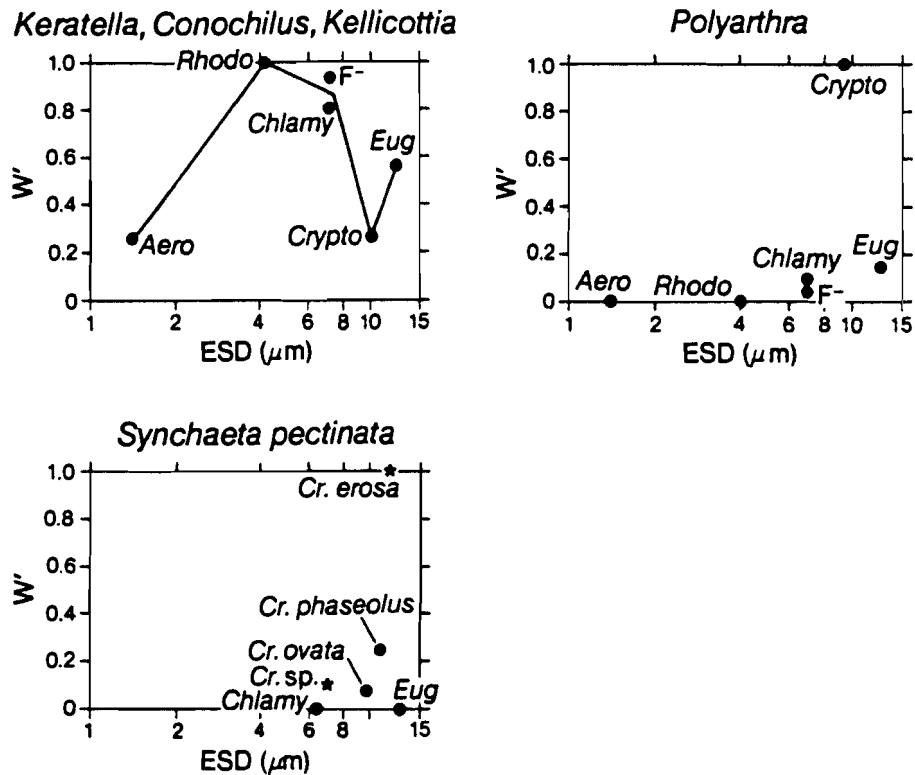
Figure 13. W' vs. equivalent spherical diameter curves for generalist rotifers *Keratella*, *Conochilus*, and *Kellicottia* (upper left) and specialist rotifers *Polyarthra* (upper right) and *Synchaeta pectinata* (lower left) from study of Gilbert and Bogdan.[124] The species of algae or bacteria used in the experiments are indicated by their abbreviations: *Aero* (*Aerobacter*), *Chlamy* (*Chlamydomonas*), F⁻ (*Chlamydomonas* without flagellum), *Crypto* (*Crypotomonas*), *Eug.* (*Euglena*), *Rhodo* (*Rhodomonas*), and *Cr.* (*Cryptomonas* with indicated species names).

In experiments with algal exudate-flavored and unflavored microspheres, *Branchionus* fed nonselectively, *Filinia* fed preferentially on 6-μm flavored spheres, and *Polyarthra, Synchaeta, Notholca,* and *Keratella* ingested few flavored or unflavored spheres.[82] The lack of feeding on spheres by the specialists *(Polyarthra, Synchaeta,* and *Notholca)* is not surprising, but the results for *Keratella,* a generalist, are surprising. In a later study, however, Rothhaupt[126] showed that the generalist *B. angularis* did not ingest 12-μm microspheres, but ingested algae of the same size, although at a lower rate than smaller algae. Perhaps *Branchionus* recognized the lack of taste of the large microsphere. Or possibly it could swallow a large elastic alga but not a large hard microsphere. Further work on feeding mechanisms is required to explain these differences.

In addition to ingesting a wide variety of particles, *Branchionus* has a selectivity for the toxic blue-green alga *Anabaena flos-aquae* equal to that of high-quality algae *(Chlamydomonas),* and can utilize this toxic alga as a sole or supplementary food source.[79,127] Rothhaupt[128] showed that selectivity in *Branchionus* was largely size dependent, and ingestion was well predicted by the EFC model.

IV. TUNICATES AND CLADOCERANS: METAZOAN FILTER FEEDERS

A. MORPHOLOGICAL DIFFERENCES AND FUNCTIONAL SIMILARITIES

Although pelagic tunicates (phylum Chordata), which are restricted to marine systems, and Cladocera (phylum Arthropoda, class Crustacea), which are largely restricted to fresh water, are very different in both taxonomic and morphological terms, most function as opportunistic filter feeders that can compete successfully with calanoid copepods. They typically filter, by sieving and other physical mechanisms (see below), a broad range of particle sizes, including picoplankton (<2 μm), and accept or reject a collected mass of particles as a unit. This implies that there is little capacity to select particles on the basis of nutritional quality. Typically, selection is a concentration-invariant function of particle size or in some cases particle size and surface properties (charge).[129-131] Many members of both groups have high weight-specific clearance rates and/or high G_{max} values, and — unlike the copepods, which must reproduce sexually — they have reproductive strategies that can rapidly turn ingested food into new individuals to exploit temporarily high food concentrations.[132,133]

B. PELAGIC TUNICATES

1. Salps and Doliolids

Salps and doliolids feed by straining particulate material through a continuously produced conical mucous net that fills much of the pharyngeal cavity.[132,134-137] This plankton net is wound up and continuously ingested. Salps, which use circumferential muscle bands for locomotion and for forcing water through the net, have higher filtering rates and can be larger than the doliolids, which use ciliary action to drive water through the nets.[132] Because of the evanescent and fragile nature of these nets, the pore-size distribution of the net is not known; however, the filtering efficiency (W') vs. particle-size curves have been determined for salps from feeding experiments using natural seston counted and sized with a Coulter counter.[135] As can be seen from Figure 14, which shows results from the largest and smallest species studied by Harbison and McAlister,[135] some salps are quite efficient at removing small particles even down to 1 μm. Observed differences in the W' curves among and within species are related to animal size: smaller salps retain smaller particles. Cinematographic observations on the feeding mechanism of the neritic doliolid *Doliolum nationalis* suggest that its filter is quite coarse, having a particle retention efficiency on the order of 50% for 4-μm particles[137] (contrast with values for benthic suspension feeders in Chapter 8).

The oceanic salp *Pegea confoederata* is able to survive on extremely low concentrations of food found in oceanic central water masses. When it is exposed to the higher particle concentrations typically found in neritic areas, feeding is disrupted because the mucous net becomes overloaded with food and breaks.[136] This breakage is thought to be a factor excluding these animals from neritic areas. This is a clear-cut example showing that the optimal-foraging narrative does not apply to all ranges of particle concentration presented by the investigator or some environments, i.e., there are "design" constraints that limit optimal behavior to certain environments.

Deibel and Paffenhofer,[137] using high-speed microcinematography, were able to describe the special mechanisms necessary to handle large particles and certain aspects of the fluid dynamics of particle capture. This appears to be a fruitful area of research, especially since the fluid mechanics of filters like these have already been worked out by Silvester.[138]
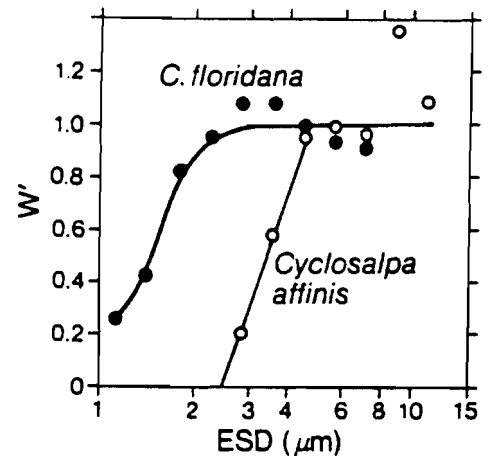
Figure 14. W' vs. equivalent spherical diameter (ESD) curves for largest species *(Cyclosalpa affinis)* and smallest species *(C. floridana)* of salps in study of Harbison and McAllister.[135] (Redrawn from Harbison, G. R. and McAllister, V. L., *Limnol. Oceanogr.*, 24, 275, 1979.)

2. Appendicularia

The mechanisms of filtration in pelagic appendicularians have recently been reevaluated by Deibel[139-142] in his studies of *Oikopleura vanhoeffeni*, a neritic cold-water species. Appendicularians feed within a complex set of mucopolysaccharide filters known as the house. The animal drives water through coarse incurrent mesh by beats of its tail, and suspended food is concentrated in a food-concentrating filter of very fine pore width (~0.2 μm). The concentrated food suspension is then forced through the pharyngeal filter, and the pharyngeal filter removes particles from suspension by sieving and adhesion. Until recently, it was believed that the pore size of the food-concentrating filter, formerly called the food collection filter, determined the particle retention efficiency. The pore-size distribution of the pharyngeal filter is much coarser, suggesting that 50% efficiency is obtained only for particles 3 μm in size. There have been no measurements of particle-size selection to test whether actual filtering efficiency matches that predicted by the pore-size distribution. *Oikopleura*, by adjusting its mouth opening, can reject part or all of the concentrated food suspension. *Oikopleura* can lower its clearance rate in high concentrations of food by intermittent pumping, thereby preventing the capture of excess food.

C. CLADOCERA
1. Single-Mode and Dual-Mode Feeders

When discussing the filter-feeding Cladocera (as opposed to the predacious Cladocera), it is necessary to distinguish between two feeding groups. The first group, the single-mode feeders (e.g., Daphniidae), collect a broad size range of particles with relatively homogeneous filter combs. The particles are sieved by the filter combs of the third and fourth trunk limbs, and setae on other appendages or structures scrape off the collected particles and move them toward the mouth.[143] The second group utilizes dual feeding modes: a raptorial mode and a filter-feeding mode.[144,145] These groups have different size-selectivity patterns and responses to other aspects of food quality; therefore, special emphasis is placed on contrasting the selectivity patterns of these two groups and relating them to their feeding mechanisms. Cladocerans are the most-studied members of the freshwater zooplankton, and we know more about their feeding biology than other freshwater zooplankton and, probably, most marine zooplankton. The filter-feeding approach of this successful group stands in marked contrast to the selective feeding of the copepods. The reasons for the dominance of one group over another in different aquatic systems have been of great interest to limnologists and probably relates, in part, to the success of these different feeding strategies in different systems.[133]

2. Food Quality
a. Small-Particle Capture Efficiency

For the single-mode feeders, selectivity for particles of different sizes is at least approximately related to the intersetule distances on the filter combs.[146-149] Anything greater than the intersetule distances is retained as long as it is not larger than the filtration apparatus can handle.[143,150] Figure 15, redrawn from DeMott,[148] shows that W' of the 1- to 2-μm-long bacterium *Aerobacter* (relative to the 6-μm-diameter *Chlamydomonas*) is related to the mesh size of the filter combs of all the single-mode feeders, but not to the dual-mode feeders *Bosmina* and *Chydorus*.

Figure 15. W' for the bacterium *Aerobacter* by different freshwater Cladocera arranged in order of increasing filter mesh width. The three size-range categories shown above the figure represent, from left to right: "high-efficiency bacteria feeders", "low-efficiency bacteria feeders", and "macrofiltrators". The dual-mode feeders are *Chydorus sphaericus* (Ch.s.) and *Bosmina longirostris* (B.l.). The single-mode feeders are *Diaphanosoma brachyurum* (D.b.), *Ceriodaphnia reticulata* (C.r.), *Simocephalus serrulatus* (S.s.), *Sida crystallina* (S.c.), *Daphnia rosea* (D.r.), *D. galeata mendotae* (D.g.m.), and *D. pulicaria* (D.p.). (Redrawn from DeMott, W. R., *Arch. Hydrobiol. Beih. Ergeb. Limnol.*, 21, 125, 1985.)

Mean Mesh Size (μm)

◄——— 0.2-0.6 ———►◄——— 0.6-1.5 —►◄-2-►

Aerobacter W'

D.b. Ch.s. C.r. D.r. D.g.m. D.p. B.l. S.s. S.c.

Species
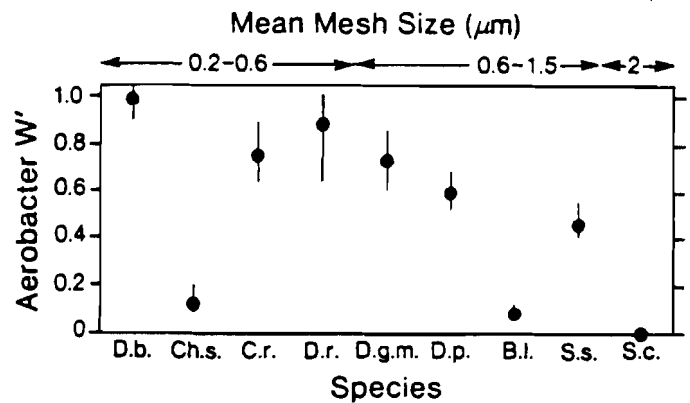
Gerritsen and Porter[129] showed that the charge and wetability of particles close to the mesh size can affect the efficiency of particle retention. This observation on surface properties has relevance to the ability of the filter to retain very small particles of different types, because electrophoretic mobility — a measure of particle (and particle-filter) repulsion — varies among algae, cyanobacteria, and bacteria; moreover, electrophoretic mobility changes with the pH of the water and dissolved organic carbon concentration.[130]

Why do different single-mode filter feeders have different mesh sizes? In addition to the correlation between mesh size and the size of the particle captured, there is evidence that coarse-meshed filter-feeding cladocerans have higher weight-specific clearance rates.[147,148] Brendelberger[147] notes that this is analogous to Fenchel's[107] observations that coarse-meshed, filter-feeding ciliates have higher weight-specific clearance rates than those having fine meshes. Perhaps there is a penalty to pay for possession of fine meshes in the form of an increased pressure drop across the "filter" system. Perhaps significantly more energy is required to push water through a system with fine meshes.

The dual-mode feeders *Bosmina* and *Chydorus* have their first two pairs of appendages modified for grasping individual large particles. As particle size increases, W' continues to increase in *Bosmina*. For example, the clearance rate on *Cosmarium* (26 × 16 × 11 μm) is six times higher than that for *Chlorella* (5 μm).[151] DeMott and Kerfoot[145] speculated that the continuous horizontal swimming of *Bosmina* may be coupled to a remote detection system for the capture of large particles.

b. Nutritional Quality of Particles

Like filter feeders in general, the single-mode feeders have limited capacity to reject individual particles. In the single-mode feeders, filtered particles travel up to the food groove to form a bolus under the labrum that is worked over and tasted prior to ingestion.[131,152] Rejection is accomplished by the first two limbs, which are not used for filtering. Gerritsen et al.[131] noted that some individual large particles could be ingested or rejected from boluses containing many particles. Excess food and colonies or filaments that clog the filtering apparatus are rejected by the abdominal claw.[81,153] Excess cells not packed in a bolus can also be flushed out of the carapace by "outwashing".[154] Carapace gape may be decreased somewhat to prevent the entry of filaments into the filter chamber.[155]

The selectivity patterns of the single-mode feeders are consistent with the limited capacity of these rejection mechanisms to regulate the nutritional quality of ingested food. The selectivities for 6-μm flavored and unflavored microspheres were identical.[82] However, later, more detailed studies show some ability of single-mode feeders to select algae or flavored microspheres over unflavored microspheres. Kerfoot and Kirk[156] showed that small single-mode feeders had somewhat higher preferences for flavored as opposed to unflavored microspheres and for small (6-μm) as opposed to large (12-μm) microspheres. Large cladocerans did not show this discrimination. Kerfoot and Kirk[156] thought this was a result of the smaller cladocerans processing the microspheres one at a time and their inefficient handling of larger microspheres. Bern[85] showed that small single-mode feeders fed on algae and microspheres at the same rate for particles of 2, 6, and 11 μm, but that 19-μm algae were preferred over 19-μm microspheres. Single-mode feeders were only partially successful in selecting against the filamentous toxic blue-green

alga *Anabaena flos-aquae* when paired with 6-µm *Chlamydomonas reinhardti*.[79] Pairing *Anabaena* with *Chlamydomonas* lowered the feeding rate on *Chlamydomonas*, through either toxic effects or inefficient rejection mechanisms that rejected *Chlamydomonas* as well. In contrast, when the filamentous diatom *Melosira* was paired with *C. reinhardti*, *Melosira* was preferred. Fulton and Paerl[157] showed that in mixtures of unicellular toxic *Microcystis* (4 µm) and *C. reinhardti*, there was no evidence of discrimination against *Microcystis*. Prior exposure to *Microcystis* did not alter selectivity, but, through its toxic effects, did lower filtering rates.

The dual-mode *Bosmina* can use chemosensory abilities to select particles but does not avoid ingesting toxic blue-green algae. DeMott[82] showed that the W' of unflavored 6-µm spheres was 0.6 relative to *C. reinhardti* of the same size. In a comparison of microspheres and algae of the same size, *Bosmina* strongly selected against 11- and 19-µm microspheres.[85] Fulton[79] observed W' values of 0.75 for *C. reinhardti* relative to toxic unicellular *Microcystis* and 0.59 relative to toxic *Anabaena*. *Bosmina* is resistant to the toxins of these algae, although it does not reproduce if either of these algae is the sole food source.[158]

c. Size, Shape, and Motility

Once a particle is captured by a filter-feeding cladoceran, it must be handled before ingestion. Many of the problems described above for copepods handling large particles of varying shapes apply here. *Diaphanosoma brachyurum*,[79] which is a high-efficiency bacteria feeder, is incapable of ingesting filamentous algae. *Daphnia* readily ingests the filamentous diatom *Melosira italica*, but not *M. italica tenuissima* because the cells of the latter cannot be separated easily by *Daphnia* for ingestion.[159] The colonial diatoms *Asterionella* and *Fragilaria* also offer difficulty for some *Daphnia* spp.[159] The dual-mode feeder *Bosmina* has very much higher selectivities for filamentous algae than for *C. reinhardti*.[79] Its first two appendages, modified for grasping large particles, undoubtedly are important in this high selectivity.

Motile microzooplankton prey like *Polyarthra*, which have vigorous escape responses elicited by cladoceran flow fields, will escape capture.[160]

3. Concentration-Variable Selectivity

As might be expected from the largely passive and mechanical selection of the single-mode feeders, selectivity for large and small particles of varying nutritional qualities does not change much with particle abundance.[76,83,161] However, Hartmann and Kunkel,[152] in a model emphasizing the multistep feeding process of *Daphia*, argued that filamentous algae will be selected against at most steps, compared to spherical algae, ;cause of problems of handling. Moreover, they hypothesized that this "behaviorally controlled" handling would lead to variable selection for mixtures of spherical and elongated algae. No reliable data are available to carefully evaluate their hypothesis.

It is a different story for the dual-mode feeder *Bosmina* feeding on mixtures of 6-µm *Chlamydomonas* and 1- to 2-µm *Aerobacter*.[161] When *Chlamydomonas:Aerobacter* concentrations were 2.5:0.25 and 0.25:2.5 µg ml⁻¹ dry weight, the respective W' values of *Aerobacter* were 0.36 and 0.073. The higher selectivity for *Aerobacter* at the higher *Chlamydomonas* concentration was a result of the clearance rate for *Aerobacter* remaining the same but that of *Chlamydomonas* dropping. This is a satiation-driven response for the raptorial feeding mode, which we could probably term an active feeding mode, since, like the copepods, response to remotely detected particles is probable. It would be of interest to know what aspect of the behavioral chain leading to ingestion is affected. Is it searching behavior, or some aspect of handling?

V. DISCUSSION: SOME INTERESTING NARRATIVES

A. OLD NARRATIVES

1. Zooplankton Are Not Peak Trackers

I have shown that copepods, cladocerans, and ciliates do not focus their efforts on the most available prey. When concentration-variable selectivity occurred, it was satiation driven and a drop in selectivity for a difficult to handle or less desirable food was observed. In the case of the less desirable food, there may not be enough of a stimulus to trigger the ingestion response when the animal is satiated. Ecologists often argue that as the animal gets hungrier, it includes more prey items in its diet and becomes less selective.[2] This assumes the implicit frame of reference of the well-fed animal.[43] The more appropriate frame of reference may be the hungry animal. More focus should be put on studying the animal's feeding behavior at very low food concentrations. As I have argued above, an appropriate perspective is to

recognize that selection is a multistep process that can be affected by motivation at each step (Figure 3). This mechanistic perspective, I believe, provides the framework for making observations useful for the development of predictive models. After we understand the mechanisms, we can ask if they have adaptive value relative to our narratives concerning optimal foraging.

2. Dynamics of Ecosystems Cannot be Described by the Size of Their Components

Size is an important variable in terms of its effect on the rates of various physiological processes, including metabolic rate and feeding rate. Also, if closely related species are of different sizes but have the same food collection systems (as, e.g., the *Diaptomus* spp. in Figure 5), allometry of the food detection, collection, and ingestion organs will lead to size-related patterns in selectivity. The W'-ESD spectrum of *D. ashlandi* is shifted to the left of the other two species because it is a much smaller species.

However, when we start comparing organisms that are not closely related, generalizations about feeding based on size become tenuous, especially when the species belong to different feeding guilds. In the latter case, different responses to other aspects of food quality such as motility, toxicity, shape, and biochemical composition will confound predictions based on size. Copepods and cladocerans, which overlap in size, do not function in the same way in ecosystems. Likewise, generalist rotifers and ciliates do not function the same way that specialist rotifers and ciliates do.

If we are going to truly understand aquatic ecosystems, we have to study the feeding mechanisms of their major components and not rely on the easy verities of size arguments. If we were studying the feeding behavior of lions on the plains of Africa, we would follow them around, watching their behavior through binoculars or recording results on video or film. We must do the same with the zooplankton: we must enter their world and follow them around. Recent advances in cinematography and videography make at least some aspects of this direct observation possible.[162]

3. Certain Metazoan Filter Feeders Can Ingest Picoplankton

Certain pelagic tunicates and cladocerans can ingest picoplankton, including bacteria. Probably more work is necessary to identify pelagic tunicates that have this ability. Clearly, only some of the Cladocera can do this. An interesting question is: Why are not more metazoan filter feeders capable of ingesting bacteria? Are there filter-design or energetic constraints that prevent their efficiently filtering bacteria? I touch briefly on the subject below when I discuss temperature and water viscosity.

B. A GREAT LAKES NARRATIVE: THE IMPORTANCE OF PHYSICS

Armed with our new information on feeding mechanisms, it is possible to tell a number of new stories about the plankton in the Great Lakes. I choose to focus on two stories, the stories about viscosity and turbulence, because these physical variables may play an important but generally unappreciated role in the evolution of aquatic communities.[25,60] In Figure 2, we have seen that as we move from oligotrophic to the eutrophic Great Lakes, dominance of the grazing community by calanoid copepods shifts to Cladocera. This shift in the annual average community structure is caused by the explosive parthenogenetic reproduction of cladocerans during the warmer months in the eutrophic lakes. This result is consistent with Muck and Lampert's[133] observations that *Diaptomus* has a higher filtering rate than *Daphnia* at low food concentrations, but that *Daphnia* has a higher maximum ingestion rate, G_{max}. The higher G_{max} is turned into high production of parthenogenic offspring in the higher particle concentrations found in eutrophic lakes.

Of course, this response depends on the size and kind of food available. Geller and Muller[163] developed a scheme to explain the seasonal succession of zooplankton on the basis of food size. They subdivided cladocerans into three groups on the basis of filter mesh size: (1) "high-efficiency bacteria feeders (0.24- to 0.64-μm mesh size)", (2) "low-efficiency bacteria feeders (1.0-1.6 μm)", and (3) "macrofiltrators (>2.0 μm)". Copepods were thrown into the macrofiltrator category because there are few cladoceran macrofiltrators. In oligotrophic lakes, macrofiltrators in the form of copepods dominate throughout the year. In mesotrophic and eutrophic lakes, copepods dominate throughout winter. In mesotrophic lakes, medium-mesh cladocerans dominate during spring through autumn. In eutrophic lakes, medium-mesh species dominate during spring and autumn, while fine-mesh species dominated during summer. Geller and Muller[163] argued that this succession was driven by the increasing importance of bacterial food, especially in the eutrophic lakes.

It seems to me that an important additional force behind Geller and Muller's[163] successional pattern could be the impact of temperature-driven changes in viscosity on the food collection system of the

copepods and cladocerans. In going from 25° to 1°C, viscosity increases by a factor of two. The pressure drop across a filter is proportional to the viscosity, μ.[115] Also, the boundary layer thickness around filter elements is proportional to $\mu^{1/2}$ and inversely proportional to $U^{1/2}$, where U is the flow rate through the filter.[164] Jørgensen et al.[165] showed that the ciliary pump of bivalves was a constant-force pump whose pumping rate dropped in accordance with this viscosity relationship. What is the nature of the pump in cladocerans? Also, increased boundary layer thickness at low temperatures might have a detrimental effect on filter function. Thus, in summer, when viscosity is less likely to be a problem, the fine-meshed cladocerans can dominate. *Diaptomus* spp. generally reproduce during winter and spring. The scanning system of copepods may be especially efficient at low temperatures. I am not aware of any experiments on cladoceran feeding at low temperatures that could be used to test these ideas. Moreover, cold water plus oligotrophic conditions may represent particularly difficult conditions for cladocerans to overcome. Algal concentrations are often low in winter. Many cladocerans escape winter by producing resting eggs. Perhaps this is their way of escaping the rigors of high viscosity and low food concentrations. The low temperatures of Lake Superior may present a year-round barrier to cladoceran domination: the average surface temperature in July is 7°C. I wonder if the seasonal and latitudinal distribution of metazoan filter feeders, in general, may be caused by temperature-related viscosity constraints operating on their filtration systems.

The other important physical question is, what is the importance of turbulence to zooplankton? Are zooplankton of large lakes adapted for turbulence, whereas zooplankton of small lakes and ponds are not? Often, young stages of copepods are found in surface waters, whereas adults are not. Does this mean these young stages are turbulence adapted, whereas adults are not?

ACKNOWLEDGMENT

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